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CARBON ASSIMILATION AS A FUNCTION OF INGESTION RATE IN LARVAL PACIFIC HERRING, *CLUPEA HARENGUS PALLASI* Valenciennes

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Abstract: During the larval stage, clupeoids and other fishes are characterized by straight, relatively undifferentiated guts. Where it has been studied in detail, the evacuation rate in these larvae appears to be directly related to ingestion rate, which is in turn related to food concentration. Qualitative assessments have suggested that the degree of digestion of food particles is inversely related to the rate of evacuation. In the present study, early larvae of the Pacific herring, *Clupea harengus pallasi* Valenciennes, were fed for 1 h upon ^{14}C-labelled rotifers, *Brachionus plicatilis* Muller, and *Artemia* nauplii at high densities. At the end of 1 h, larvae were transferred to six food densities, ranging from 0 to 10 unlabelled prey · ml^{-1}. After 22 h, larvae were removed from the feeding tanks and sacrificed. The labelled carbon remaining in the larvae as a function of the percent consumed after the 1-h feeding interval was used as an index of carbon assimilation. The percent carbon retained decreased significantly with increasing food concentration. Larval herring thus decrease carbon assimilation from individual food particles at high food densities. The magnitude of increasing ingestion, however, more than compensates for the decreased carbon assimilation, and larvae gain greater total energy under conditions of high food concentration. The results support the suggestion that clupeoid larvae are adapted to utilize high food concentrations associated with plankton patches in the pelagic environment.

INTRODUCTION

Survival of larval fishes is dependent upon adequate food resources. In early larvae, high mortality resulting from low food densities may result in critical periods which can ultimately affect year class strength (Hjort, 1914). More recent work demonstrates that the food must be of the appropriate type (Scura & Jerde, 1977) and must also be distributed on the appropriate scale (Lasker, 1975; Lasker & Zweifel, 1978). The scale of distribution results in varying concentrations of prey, which are apparently utilized differently by larvae of different fish taxa. Larvae of the clupeoid *Engraulis mordax* require food densities greatly in excess of average densities found in the sea (O'Connell & Raymond, 1970). Lasker (1975) later showed that sufficient food densities existed in specific patches in the sea, and Hunter & Thomas (1974) demonstrated that larvae alter search behavior to increase the probability of remaining in those patches once found.

The work of Houde (1978), and Houde & Schekter (1981, 1983) suggests that the above pattern does not characterize all larval fishes. They compared the survival, growth, and energetics of larval clupeiform, pleuronectiform, and perciform fishes and demonstrated striking differences. For all three taxa, the ration consumed depended on

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food density; the clupeiform could consume the highest ration at high food density, but it had the lowest growth efficiency (Houde & Schekter, 1981, 1983). Furthermore, to achieve the same growth and survival as the other taxa, 2–10 times the food density was necessary for the clupeiform, *Anchoa mitchilli* (Houde, 1978).

The above observations on clupeiform larvae support the contention of Griffiths (1975) that larval fish are number maximizers, consuming prey at nearly the rate they are encountered, as opposed to energy maximizers, which forage and process prey to maximize net energy. Other work supports this idea. Werner & Blaxter (1980), working with larval *Clupea harengus*, noted marked increases in evacuation rate with increasing prey concentration. Visual observations showed that digestion was poor at high prey densities, and they suggested that assimilation may decrease with increasing prey density. Similarly, Chitty (1981) noted food residence times as low as 7 min in the gut of larvae of the clupeoids *Anchoa mitchilli* and *A. lamprotaenia*. Thus, as prey density varies, the energy extracted from individual prey may change. The magnitude of this change in assimilation, however, is unknown. If low enough, additional prey may result in little net gain in energy with increasing ration. In other continuous feeders, this has been termed superfluous feeding (Beklemishev, 1962). In the present study we estimate an index of carbon assimilation and total carbon intake in larvae of the Pacific herring, *Clupea harengus pallasi* Valenciennes, as a function of prey concentration.

Materials and Methods

Herring larvae were laboratory-reared from eggs which had been spawned naturally on inter- and subtidal algae in Yaquina Bay, Oregon on 15 April 1982. Culturing and all experiments were conducted in a temperature and light-controlled room (10 °C; 9 h light : 15 h dark) in filtered sea water at 15‰ salinity. After hatching, larvae were maintained on the rotifer, *Brachionus plicatilis*, cultured after the methods of Theilacker & McMaster (1971).

B. plicatilis and the naupliar stage of *Artemia salina*, both common food organisms used in larval fish rearing, were labelled with ^{14}C following methodology of Sorokin (1966) and Govoni *et. al.* (1982). The unicellular marine alga, *Isochrysis* sp. (Ewart & Epifanio, 1981), was cultured for 1 wk at 18 °C and pH 8.8 in 2.8 l of media with 200 μCi ^{14}C sodium bicarbonate (New England Nuclear). *Brachionus* were innoculated into a labelled algal culture at 16 rotifers · ml^{-1} and allowed to incorporate the isotope for 1 wk; newly-hatched *Artemia* nauplii were fed labelled algal culture for 48 h at 54 nauplii · ml^{-1}. Labelled food organisms were acclimated overnight to 10 °C and allowed to evacuate guts of labelled algae prior to feeding them to the larval herring.

On Day 16 post hatching, ≈300 herring larvae, with mean notochord length (NL) of 10.3 mm, were transferred to a 10-l black plastic pot and held in darkness for 15 h without food, which allowed complete gut evacuation. In the morning, larvae were fed with labelled *Brachionus* at 30 rotifers · ml^{-1}. Six larvae were removed from the feeding

tank at each of the following intervals: 0, 0.25, 0.5, 0.75, 1, and 2 h after initial feeding to establish a time–ration relationship. At each time, these larvae were divided into two replicates of three larvae each, which were prepared for liquid scintillation counting (LSC). After 1 h of feeding on labelled prey, other groups of larvae were transferred to 10-l tanks containing non-labelled *Brachionus* at concentrations of 0, 0.2, 0.5, 1.0, 5.0, and 10.0 rotifers $\cdot$ ml^{-1}. Great care was taken during transfers to ensure that only larvae, and no labelled food, were transferred. At 22 h after larvae were removed from labelled food, when intestines in all feeding groups were free of labelled food, three replicates of five larvae from each concentration were prepared for LSC.

Similar feeding experiments were conducted using the larger food organism, *Artemia* nauplii. At 31 days post hatching, herring larvae (mean NL of 13.8 mm) were starved as above prior to being fed with ^{14}C-labelled *Artemia* at 15 nauplii $\cdot$ ml^{-1}. Larvae were taken from the feeding tank on the same schedule as above, but with three replicates of two larvae each prepared for LSC. Again, larvae were transferred to tanks containing non-labelled food 1 h after feeding began. The densities for the *Artemia* experiments were 0, 0.03, 0.3, 1.5, 3, and 10 nauplii $\cdot$ ml^{-1}. Three replicates of four larvae per food density were prepared for LSC 22 h after being transferred from the labelled food tanks. Again, all labelled food was evacuated from the larval guts.

Larval herring sampled for LSC were removed from the experimental tanks with a large-bore pipette, placed into a watch glass, and handled with forceps to avoid contamination with labelled food. Larvae were digested in scintillation vials with 1 ml of tissue solubilizer (Beckman BTS) for 24 h at 55 °C, cooled to room temperature, and counted in 10 ml of Ready-Solv EP fluor (Beckman). Chemiluminescence was reduced by the addition of 0.1 ml glacial acetic acid to each sample and by dark adapting samples prior to counting. Both labelled food organisms were analyzed for activity prior to feeding experiments. An aliquot of 10 ml was removed from each of the two labelled cultures; food organisms were enumerated and filtered onto tared glass fiber filters. After drying overnight at 55 °C, the filters were weighed to the nearest μg and solubilized and counted as previously described. Counts per minute (CPM) were corrected for counting efficiency by developing a quench curve with standard, calibrated samples of ^{14}C prepared in a manner similar to experimental samples, and were expressed as disintegrations per minute (DPM).

To account for respired ^{14}C and that defecated as particulate organic ^{14}C, after 1 h feeding on labelled *Artemia*, three larvae were placed in each of four Gilson respirometer flasks with 0.5 ml of 10% KOH in the center well with filter paper as a trap for carbon dioxide; larvae were held in 8.0 ml of sea water. After removal of larvae with forceps, the liquid in the vessel was acidified with 0.5 ml of concentrated sulfuric acid, immediately sealed, and held for 2 h while carbon dioxide was adsorbed onto the filter paper. Samples prepared for LSC from each of the four replicates included (1) the filter paper with KOH, (2) three larvae solubilized as above, (3) particulate carbon collected on 0.3-μm glass fiber filters and solubilized, (4) a blank filter with filtrate passed through, and (5) 1 ml of filtrate to assay for dissolved organic ^{14}C.

For describing relationships between variables, logarithmic and exponential functions were fit to data. Where percentages were used, values were arcsin transformed prior to analysis.

RESULTS

Larval herring readily fed during the experiments on both labelled and unlabelled *Brachionus plicatilis* and *Artemia salina* nauplii. Because larval herring are continuous feeders in daylight, the food uptake curves should be approximately asymptotic; for our experiments it was important to choose a time slightly before the gut was completely full to prevent defecation of ^{14}C labelled prey. For both *Brachionus* and *Artemia*, uptake of ^{14}C as a function of time was characterized by asymptotic curves (Fig. 1). The curves are described by the following relationships:

$$\textit{Brachionus}: (\text{DPM} \cdot \text{larva}^{-1}) = 1059.7[\ln(t + 1)] - 401.8$$
$$n = 12,\ r^2 = 0.68\ (P < 0.01)$$
$$\textit{Artemia}: (\text{DPM} \cdot \text{larva}^{-1}) = 532.6[\ln(t + 1)] + 356.5$$
$$n = 18,\ r^2 = 0.31\ (P < 0.025)$$

These relationships predict ^{14}C consumed at 60 min to be 3955 DPM · larva^{-1} for *Brachionus* and 2546 DPM · larva^{-1} for *Artemia*. Given the mean value of ^{14}C in *Brachionus* (89.3 DPM) and *Artemia* (684.9 DPM), this suggests that mean consumption was 44.3 *Brachionus* and 3.7 *Artemia* during the 1-h period of feeding on labelled food. These are reasonable estimates of feeding rates at these densities for larvae near this age (Werner & Blaxter, 1980).

In all feeding experiments, the 22-h period after exposure to ^{14}C-labelled food was sufficient to result in complete evacuation of labelled particles, even at the zero food level, as shown by microscopic observations. Where larvae were fed labelled *Brachionus*, the amount of carbon retained (in DPM · larva^{-1}) decreased significantly with increasing food density (Table I; Fig. 2). Expressed as a percentage of the ingested ^{14}C

TABLE I

Results from feeding experiments with *Brachionus plicatilis*: the caloric content of *Brachionus* was calculated from the mean value in Theilacker & Kimbrell (1984); each of the three replicates was based upon the mean of five larvae; the value represents the ^{14}C retained after 22 h.

Food density (*Brachionus* · ml^{-1})	cal · l^{-1}	*N*	Mean DPM · larva^{-1}	SE
0	0	3	1892	242
0.2	0.26	3	1734	125
0.5	0.66	3	2032	313
1.0	1.32	3	1807	40
5.0	6.60	3	1346	19
10.0	13.20	3	1523	119

(calculated from the relationship in Fig. 1A) and arcsin transformed, the relationship is expressed as follows:

$$\arcsin(C) = 43.467 \exp[-0.074 \ln(f + 1)]$$
$$n = 18,\ r^2 = 0.313\ (P < 0.025)$$

where C = percent ingested carbon and f = food density (*Brachionus* · ml^{-1}).

Similar results were observed with herring larvae fed *Artemia* nauplii. Again, ^{14}C retained (DPM · larva^{-1}) decreased from very high values in the experiment with no

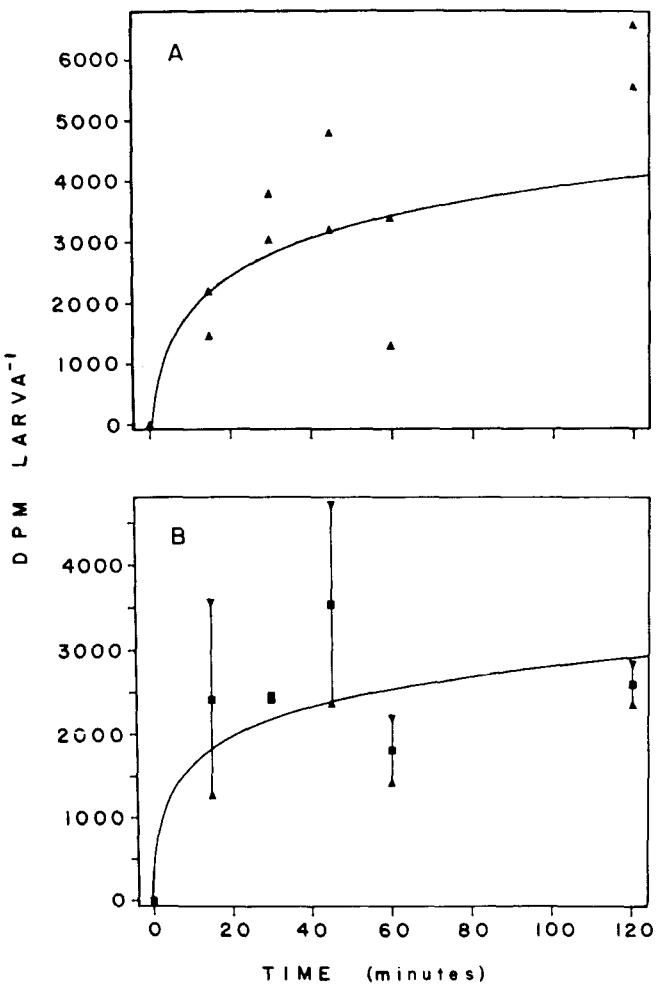

Fig. 1. Uptake of ^{14}C by larval *Clupea harengus pallasi* as a function of time: A, 4-wk-old larvae feeding on *Brachionus*, the points represent the two replicates at each time; B, 6-wk-old larvae feeding on *Artemia* nauplii, points shown are the means of three replicates ± 1 SE; in both cases, the fitted curve is described in the text.

food (Table II; Fig. 3). The range of predicted values of carbon retained was generally greater for *Artemia* than for *Brachionus*. This may be due to the fact that the protocol for labelling *Brachionus* with ^{14}C required 7 days and population growth, whereas that for *Artemia* took only 30 h; thus significant proportions of the ^{14}C in *Brachionus* may

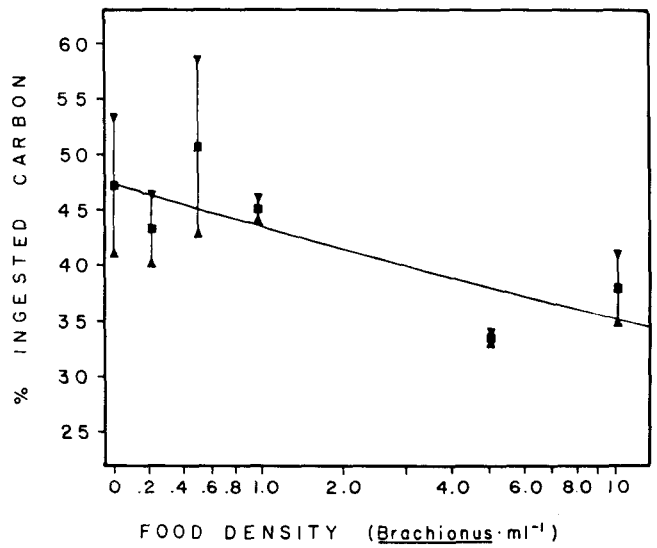

Fig. 2. The percentage of ingested ^{14}C retained per herring larva after 22 h feeding on non-labelled *Brachionus*: the data are fit with an exponential curve described in the text; data points are means of three replicates ± 1 SE.

TABLE II

Results from feeding experiments with *Artemia salina* nauplii: the caloric content of *Artemia* was calculated from the value of 0.00937 cal · nauplius $^{-1}$ in Benijts *et al.* (1975); each of the three replicates was based upon the mean of four larvae; the value represents the ^{14}C retained after 22 h.

Food density (*Artemia* · l^{-1})	cal · l^{-1}	*N*	Mean DPM · larva^{-1}	SE
0	0	3	2091	302
0.03	0.28	3	1179	228
0.30	2.81	3	1209	172
1.50	14.06	3	736	128
3.00	28.11	3	1066	83
10.00	93.70	3	956	183

have been in indigestible lorica. Indeed, in similarly labelled *Brachionus*, Govoni (1980) noted 66% of the ^{14}C in protein, 7% in lipids, 4% in carbohydrates, and the remainder in unextracted, and probably undigestible, components. An alternative explanation is related to size and foraging costs. Individual *Brachionus* are smaller and contain only

14% the calories of *Artemia*; thus, foraging costs to obtain a given ration are higher and the respiratory utilization of ^{14}C during the 22-h period may be higher. Expressed as a percentage of the ingested ^{14}C (calculated from the relationship in Fig. 1) and arcsin transformed, the relationship is as follows:

$$\arcsin(C) = 47.80 \exp[-0.144 \ln(f + 1)]$$
$$n = 18, r^2 = 0.208 (P < 0.05)$$

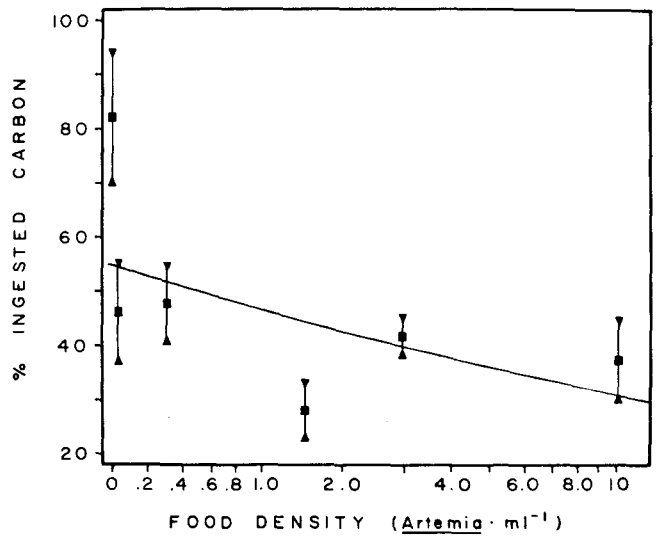

Fig. 3. The percentage of ingested ^{14}C retained per herring larva after 22 h feeding in non-labelled *Artemia* nauplii: the data are fit with an exponential curve described in the text; data points are means of three replicates ± 1 SE.

The percent carbon retained may only be considered as an index of assimilation (Govoni *et al.*, 1982), since short-term carbon pools may be recycled or used as respiratory substrates (Conover & Francis, 1973). The experiments with ^{14}C *Artemia* fed larvae in retention chambers were conducted to estimate the carbon retained, respired, and defecated (Table III). The dissolved ^{14}C remaining after acidifying the filtrate represented an average of 8.2% of the total ^{14}C in the retention chambers. The particulate carbon from the retention chambers may be considered as non-assimilated feces; thus our estimate of assimilation is 58.5% at zero food density with *Artemia*. Of this amount, 19.5% is respired during the 22-h interval between feeding with labelled food and sacrifice. This value allows us to adjust the carbon retained after 22 h to a closer index of carbon assimilation for experiments with *Artemia*.

Discussion

Two other studies have been conducted on energetics of larval fishes using ^{14}C as a tracer to follow carbon uptake and assimilation after the general techniques of Sorokin (1966); both studies, however, have considered percoid larvae. Sorokin & Panov (1966) studied the energetics of the larvae of the freshwater fish *Abramis brama* and noted assimilation values of ≈ 75–80% of ingested carbon. Govoni *et al.* (1982), using a larval sciaenid (*Leiostomus xanthurus*), observed a mean carbon absorption of 87.6%. While neither of these studies estimated the effect of varying food density, they observed no change in assimilation with increasing larval age. In our study, the estimate of carbon assimilation depends upon food density. The estimates for herring larvae feeding on *Artemia* from Fig. 3, corrected for respiration (Table III), decrease exponentially from 68.2% at 0.001 *Artemia* · ml^{-1} to 38.5% at 10.0 *Artemia* · ml^{-1}. Assuming the same respiratory fraction for larvae feeding on *Brachionus*, corrected estimates from Fig. 2 are 58.8% at 0.001 *Brachionus* · ml^{-1} to 43.7% at 10 *Brachionus* · ml^{-1}. The high values in Govoni *et al.* (1982) may have resulted from using retention chambers free from food, resulting in maximum assimilation under non-steady state feeding conditions. Our lower estimate of assimilation may relate to the type of larva; clupeoid larvae, such as *Clupea harengus*, have straight guts with no intortion (O'Connell 1981). Houde & Schekter (1981, 1983) observed the lowest growth efficiency in clupeiform larvae among larvae from three orders. Thus our estimates of carbon assimilation are near expected levels.

The decrease noted in assimilation efficiency (Figs. 2,3) correlates well with past qualitative observations on clupeoid larvae, particularly those of Werner & Blaxter (1980). They noted decreasing evacuation times with increasing prey density for *Clupea harengus* larvae feeding on *Artemia* nauplii. Similarly, Laurence (1971) noted nearly a doubling of evacuation time when larvae with a full gut were deprived of food as compared to those which were fed. Larval herring and many other fish larvae are continuous feeders in daylight; other continuously feeding animals show similar responses. Doohan (1973) noted that when food was in excess, assimilation efficiency in the rotifer *Brachionus plicatilis* decreased markedly; this effect was due to particles passing through the gut so rapidly that they were not effectively digested. Similarly, Reeve *et al.* (1978) observed decreasing assimilation with increasing food density in a ctenophore. Cushing (1959) suggested that copepods may consume 5–10 times more food than they need. This phenomenon has been described as "superfluous feeding" (Beklemishev, 1962), defined as when continuously feeding animals do not increase assimilation in response to an increase in standing stock of their food. Conover (1966), however, observed no decrease in assimilation with increasing ingestion and stated that superfluous feeding "does not normally occur in nature". For fish larvae, however, it should be pointed out that feeding does not occur in the dark; thus the effects of any superfluous feeding would not be as great as in a true continuous feeder.

The important question about the reduced assimilation efficiency is its interaction with feeding rate. Werner & Blaxter (1980) observed defecation of live *Artemia* nauplii

from the guts of larval *Clupea harengus* at the highest food densities tested. If the decrease in assimilation efficiency is not counteracted by a greatly increased feeding rate, then total carbon assimilated may decrease, a situation similar to that of superfluous feeding (Beklemishev, 1962). Werner & Blaxter (1981) described the feeding rates of larval *Clupea harengus* as a function of age. As a function of food density (in calories $\cdot l^{-1}$), the data for 6-wk-old larvae fit a model of exponential increase as follows:

$$\text{cal} \cdot \text{h}^{-1} = 0.0392 \exp[0.2915 \ln (\text{cal} \cdot l^{-1})]$$
$$n = 5,\ r^2 = 0.932\ (P < 0.001)$$

This relationship predicts increasing consumption from 0.005 cal $\cdot$ h^{-1} at a food level of 0.001 cal $\cdot l^{-1}$ to 0.150 cal $\cdot$ h^{-1} at 100.0 cal $\cdot l^{-1}$ (Fig. 4). The relationship between *Artemia* density and the percent carbon retained (Fig. 3) was recalculated after changing *Artemia* density to cal $\cdot l^{-1}$ (after Benijts *et al.*, 1975) and correcting the percent ingested

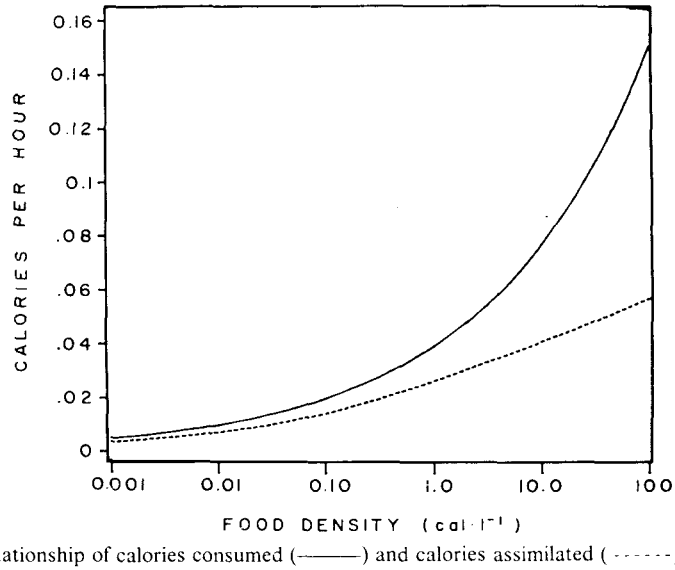

Fig. 4. The relationship of calories consumed (———) and calories assimilated (- - - - - -) as a function of food density for 6-wk-old larval *Clupea harengus* feeding on *Artemia* nauplii: the solid line is based on the equation given in the text calculated from Werner & Blaxter (1981); the dashed line is the product of this relationship with assimilation calculated from the present study.

TABLE III

Distribution of labelled carbon after 22 h in an isolation flask: each flask contained three larvae; the particulate fraction (retained on a 0.3-μm glass fiber filter) represents the feces; CO_2 represents respiration by larvae over the 22 h; carbon assimilation is therefore represented by the sum of (larva + CO_2).

Source	*N*	Mean % of total	SE
Larva	4	47.1	4.4
CO_2	4	11.4	0.6
Particulate	4	41.5	5.0

carbon to assimilation efficiency based upon respiration (Table III). The resulting relationship,

$$\arcsin(\text{assimilation}) = 58.64 \exp[-0.0953 \ln(\text{cal} \cdot \text{l}^{-1} + 1)]$$
$$n = 18,\ r^2 = 0.334\ (P < 0.01)$$

when multiplied by feeding rate, gives the calories assimilated per hour as a function of food density (lower curve, Fig. 4). The results suggest that total assimilation continues to increase despite a decreasing assimilation efficiency. When taken together, these curves would suggest that although growth may continue to increase, gross growth efficiency should decrease at high food concentrations and ingestion rate. Checkley (1982) observed increasing gross growth efficiency with increasing ingestion rate in *Clupea harengus* larvae, but suggested that gross growth efficiencies would decrease at higher ingestion rates. This is similar to gross growth efficiencies in juvenile and adult fishes, which typically decrease above some optimum ration (Brett & Groves, 1979; Boehlert & Yoklavich, 1983). Our data therefore support a departure from Blackman kinetics, where ingestion alone limits growth (Condrey, 1982).

Larval fishes depend upon patchiness of both conspecifics (Hewitt, 1981) and of prey (Hunter, 1981) to different degrees. Lasker (1975, 1978) demonstrated that first-feeding larvae of *Engraulis mordax* depend upon a stable ocean for development of the patches with appropriately sized food particles at densities of 20–40 $\cdot$ ml^{-1}. These high densities are necessary for survival (O'Connell & Raymond, 1970; Hunter, 1972; Lasker & Zweifel, 1978). Larval stages of clupeoids, such as anchovies and herrings, are apparently able to exploit these patches by continually increasing ingestion rate. Energetic analysis suggests a decrease in assimilation and gross growth efficiency (Houde & Schekter, 1980, 1981, 1983; present study); thus, as other continuous feeders, these clupeoid larvae fit the characterization of number maximizers (Griffiths, 1975). Within the constraints of uniformly sized prey in our experimental system, *Clupea harengus* larvae also maximize energy through maximizing numbers.

Acknowledgements

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